DOCUMENTED PLANT CHROMOSOME NUMBERS 1989: 1. CHROMOSOME NUMBERS IN MEXICAN ASTERACEAE WITH SPECIAL REFERENCE TO THE TRIBE TAGETEAE

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ABSTRACT

Chromosome counts are reported for 24 species of Mexican Asteraceae, 12 of these previously unreported. Newly reported counts include *Stevia latifolia*, $n=45$ I; *S. lucida* var. *bipontini*, $n=12$ II; *Desmanthodium fruticosum*, $n=17$ II; *Viguiera potosina*, $n=17$ II, *Dyssodia glandulosa*, $n=13$ II; *Geissolepis suadaefolia*, $n=8$ II; *Gymnolaena oaxacana*, $n=13$ II; *Leucactinia bracteata*, $n=16$ II; *Machaeranthera stenophylla*, $n=4$ II; *Porophyllum calcicola*, $n=12$ II; and *Pinaropappus multicaulis*, $n=9$ II. Reports for species of *Desmanthodium*, *Geissolepis* and *Leucactinia* represent new generic counts. Chromosome counts are reported for six species in four genera of the tribe Tageteae and are compared with all numbers previously reported in the tribe. When deemed appropriate, phyletic digressions are made.

Numerous chromosome reports for the large family Asteraceae are available in the literature. Indeed, attempts to ascertain the chromosome counts reported for a given large genus or group of several moderate-sized genera may necessitate several hours of patient search among the 10 or more available texts for this purpose. Because of this, it is becoming increasingly difficult to know if newly obtained chromosome counts have been reported. With this as an introduction, we report here counts for 24 species of Mexican Asteraceae (Table 1). Twelve of these represent previously unreported taxa, and three, *Desmanthodium Geissolepis* and *Leucactinia*, represent new generic reports.

METHODS AND MATERIALS

Nearly all of the chromosome counts were made from bud material by the senior author using standard acetocarmine squash techniques. Voucher specimens (Table 1) are on deposit at the University of Texas Herbarium (TEX).

DISCUSSION

EUPATORIEAE—Chromosome counts for *Stevia latifolia* ($n=45$ univalents), suggest that the species is an asexual apomict, much as suggested by its pollen grains (Grashoff 1972). The count for *Stevia lucida* var. *bipontini* ($n=12$ II) is the same as that of *S. l.* var. *lucida* (Grashoff et al. 1972).

ASTEREAE—Counts for the several species listed in Table 1 are consistent with previous reports. The counts for *Geissolepis suadaefolia* ($n=8$ II) and *Machaeranthera stenophylla* ($n=4$ II) are newly reported. The count for the monotypic *Geissolepis* is especially noteworthy in that its tribal position is conjectural. Largely because of its chaffy receptacle, the species was originally positioned in the tribe Heliantheae, but Robinson (1981) placed it in the tribe Astereae, where it appears to be properly positioned.

Geissolepis, however, appears to be strongly isolated from other American Astereae. It is distinct in its combination of a prostrate, succulent habit, sparsely short-pilose, eglandular vestiture, strongly developed resin canals on the phyllaries, achenes and disc corollas, achenial trichomes with bifurcate, sharply hooked apices, pappus of scales with the margins uncinate-ciliate, and its chromosome number of $n=8$ pairs.

Among the white- and blue-rayed members of the tribe, *Geissolepis* shows at least a vague similarity to *Astranthium* ($x=4$, 5) and particularly to *Aphanostephus* ($x=4$, 5) in its conical receptacles, peculiar achenial trichomes, and chromosome number.

HELIANTHEAE—Counts for the eight species listed in Table 2 are consistent with previous reports; those for *Desmanthodium fruticosum* ($n=17$ II) and *Viguiera potosina* ($n=17$ II) are newly reported.

LACTUCEAE—Counts for *Pinaropappus multicaulis* ($n=9$ II) have not been previously reported.

TAGETEAE—Counts for *Dyssodia glandulosa* ($n=13$ II), *Gymnolaena oaxacana* ($n=13$ II), *Leucactinia bracteata* ($n=16$ II), and *Porophyllum calcicola* ($n=12$ II) have not been previously reported; that for *Leucaetinia* ($n=8$ II) being a new generic report.

As noted in the introduction, it is becoming increasingly difficult to assess the chromosomal status of generic or suprageneric taxa. For this reason, and because of our interest in the systematics of this largely Mexican group, we present an "update" on the chromosomal reports for the tribe Tageteae (Table 2).

Strother (1977) presented a systematic review of the tribe Tageteae. He recognized 16 "accepted genera", as follows. For each of these we have listed base chromosome numbers as recounted in our Table 2.

Adenopappus	no counts
Chrysactinia	$x=15$
Dyssodia	$x=7,8,13$
Gymnolaena	$x=13$

Harnackia	no counts
Hydropectis	no counts
Lescaillea	no counts
Leucactinia	$x=8$
Nicolletia	$x=10$
Pectis	$x=12$
Porophyllum	$x=11,12,15$
Schizotrichia	no counts
Strotheria	$x=8$
Tagetes	$x=11,12,18$
Urbinella	$x=8$
Vilobia	no counts

An additional genus, *Hydrodyssodia*, recently proposed by Turner (1988) has not been counted. In addition, we would add to this assemblage the genus *Chaetymenia* (chromosome number unknown), which Rydberg (1914) positioned in the subtribe Jaumeinae. Robinson (1981) did not account for this genus in his revision of the subtribal limits of the tribe Heliantheae (within which he positioned the Tageteae as a subtribe).

Base chromosome numbers are now known for 10 of the 18 above-mentioned genera. While most of the small genera are monobasic, several larger genera (with the exception of *Pectis*) are multibasic. Thus, *Porophyllum* (sensu Johnson, 1969) has base numbers of $x=11$, 12, and 15, and is possibly polyphyletic. While those few species with $x=11$ may be dysploid derivatives of $x=12$, it is more difficult to reconcile the base number of $x=15$, which is found in *P. crassifolium* and *P. tridentatum*, both rather atypical members of that genus. We suggest that the latter might be more closely related to *Nicolettia* ($x=10$). The count for *P. greggii* ($n=18$ II) is enigmatic because the species clearly relates to *P. scoparium* ($n=12$ II). It is possibly a derived triploid on a base of $x=12$. Indeed, Johnson (1969) thought *P. greggii* to be of hybrid origin (*P. gracile n P. scoparium*). This would be consistent with the chromosomal data, *P. gracile* with $n=24$, *P. scoparium* with $n=12$, the ancestral hybrid derivative being $n=18$.

Tagetes, with base numbers of $x=11$ and 12, seemingly has a base number of $x=12$, because species on a base of $x=11$ are relatively few and specialized.

By far the most complex genus chromosomally is *Dyssodia*. Strother (1969) originally treated the genus in its broad sense. So treated, the genus can be shown to be multibasic with $x=7,8$ and 13.

More recently, Strother (1986) provided a rather drastic renovation of his concept of *Dyssodia* (sensu 1969). Instead of the more inclusive *Dyssodia* accepted in his earlier assessments (1969, 1977), he split the group into

TABLE 1. Chromosome numbers of Mexican Asteraceae.

Species	*Voucher*	*Chromosome Number*
EUPATORIEAE		
Barroetea pavonii A. Gray	Guerrero: *T15878*	*n* = 9II
	Puebla: *T15897*	*n* = 9II
**Stevia latifolia* Benth.	Puebla: *T15891*	*n* = 45I
**Stevia lucida* var. *bipontini* B.L. Rob.	Puebla: *T15906*	*n* = 12II
ASTEREAE		
Erigeron unguiphyllus Nesom	San Luis Potosi: *N6653*	*n* = 9II
Geissolepis suaedifolia B.L. Rob.	San Luis Potosi: *N6634*	*n* = 8II
Gutierrezia alamani var. *megacephala* (Fern.) Lane	Chihuahua: *N6463*	*n* = 8II
Machaeranthera crutchfieldii B. Turner	Nuevo Leon: *N6753*	*n* = 4II
**Machaeranthera stenoloba* (Greene) Shinners	Chihuahua: *N6535*	*n* = 4II
Machaeranthera turneri R.C. Jackson	Chihuahua: *N6543a*	*n* = 5II
HELIANTHEAE		
Aldama dentata Llave	Puebla: *T15889*	*n* = 17II
**Desmanthodium fruticosum* Greenm.	Guerrero: *T15876*	*n* = 17II
Lagascea rigida var. *mociniana* (DC.) Stuessy	Guerrero: *T15869*	*n* = 17II
Lasianthaea ceanothifolia (Willd.) Becker var. *ceanothifolia*	Morelos: *N6764*	*n* = ca. 10II
Montanoa frutescens DC.	Morelos: *N6758*	*n* = ca. 19II
Sabazia humilis (H.B.K.) Cass.	Morelos: *Wells 1*	*n* = 4II
**Viguiera grammatoglossa* DC.	Puebla: *T15905*	*n* = 17II
**Viguiera potosina* Blake	San Luis Potosi: *N6678*	*n* = 17II
TAGETEAE		
**Dyssodia glandulosa* (Cav.) O. Hoffm.	Puebla: *T15894*	*n* = 13II
Dyssodia porophyllum (Cav.) Cav.	Guerrero: *T15868*	*n* = 13II
**Gymnolaena oaxacana* (Greenm.) Rydb.	Puebla: *T15408*	*n* = 13II
**Leucactinia bracteata* (S. Wats.) Rydb.	Nuevo Leon: *N6793*	*n* = 16II
**Porophyllum calcicola* Rob. & Greenm.	Guerrero: *T15874*	*n* = 12II
Porophyllum linaria (Cav.) DC.	Puebla: *T15902*	*n* = 12II
	Puebla: T15910	n = 12II
LACTUCEAE		
**Pinaropappus multicaulis* Brandegee	San Luis Potosi: *N6675*	*n* = 9II

Voucher numbers preceeded by T are those of *Turner*; those preceeded by N are those of *Nesom*.
*Represent taxa previously unreported

TABLE 2. Update on chromosome numbers in tribe Tageteae.

Genera	Species or variety	Reference	Chromosome Number
Chrysactinia			
	mexicana	Keil & Stuessy (1977)	$n = 15II$, $15I$
	mexicana	Strother (1976)	$n =$ ca45
	pinnata	Powell & Turner (1963)	$n = 15II$
	truncata	Sundberg et al. (1986)	$n = 15II$
Dyssodia			
	acerosa		$n = 8II$
	(Fourteen populations of this species have been counted: 7 of these are reported as $x = 8$ pairs and 7 with $x = 13$ pairs). Strother (1969), Turner et al. (1973), Keil & Stuessy (1977), Powell & Powell (1977), Brown & Thompkins (1982), Parfitt et al. (1985).		$n = 13II$
	anomala	Strother (1969)	$n = 7II$
	anomala	Keil and Pinkava (1976)	$n = 7II$
	anthemidifolia	Strother (1969)	$n = 7II$
	appendiculata	Strother (1983)	$n = 13II$
	aurea	Strother (1969)	$n = 8II$
	aurea	Keil & Stuessy (1975)	
	concinna	Strother (1969)	$n = 8II$
	cooperi	Strother (1969, 1976)	$n = 13II$
	decipiens	Strother (1969, 1972, 1976)	$n = 13II$
	decipiens	Keil et al. (1988)	$n = 13II$
	gentryi	Strother (1969)	$n = 8II$
	glandulosa	present paper	$n = 13II$
	littoralis	Strother (1972)	$n = 7II$
	micropoides	Strother (1969)	$n = 8II$
	micropoides	Keil & Pinkava (1976)	$n = 8II$
	montana	Strother (1983)	$n = 13II$
	neomexicana	Strother (1969)	$n = 7II$
	papposa	Strother (1969)	$n = 13II$
	papposa	Grashoff et al. (1972)	$n = 13II$
	papposa	Urbatsch (1974)	$n = 13II$
	papposa	Keil & Stuessy (1975)	$n = 13II$
	papposa	Keil et al. (1988)	$n = 13II$
	pentachaeta		
	var. *helenidium*	Strother (1969)	$n = 13II$
		Keil & Stuessy (1975)	$n = 16II$
		Keil & Pinkava (1976)	$n = 13II$
		Keil et al. (1988)	$n = 13II$
	var. *hartwegii*	Strother (1969)	$n = 26II$
	var. *pentachaeta*	Strother (1969)	$n = 13II$
		Powell & Powell (1978)	$n = 8II$
	var. *puberula*	Strother (1969)	$n = 13II$
	pinnata	Strother (1969)	$n = 13II$
		Keil & Stuessy (1977)	$n = 13II$
	porophylloides	Strother (1969, 1972)	$n = 13II$
		Keil & Pinkava (1976)	$n = 13II$
		Pinkava & Keil (1977)	$n = 13II$
		Gallagher & Parfitt (1982)	$n = 13II$

(TABLE 2 continued)

porophyllum		
var. *cancellata*	Strother (1969)	$n = 13II$
	Powell et al. (1975)	$n = 13II$
	Keil & Stuessy (1977)	$n = 13II$
	Pinkava & Keil (1977)	$n = 13II$
var. *porophyllum*	Strother (1969)	$n = 13II$
sanguinea	Strother (1969)	$n = 13II$
setifolia	Strother (1969)	$n = 13, 26II$
	Keil & Stuessy (1977)	$n = 26II$
speciosa	Strother (1972)	$n = 13II$
	Turner et al. (1973)	$n = 13II$
	Gallagher & Parfitt (1982)	$n = 13II$
tagetiflora	Strother (1969)	$n = 13II$
	Keil & Stuessy (1977)	$n = 13II$
	Keil et al. (1988)	$n = 13II$
tagetoides	Strother (1969)	$n = 13II$
tenuifolia	Strother (1969)	$n = 8II$
	Gupta & Gill (1983)	$n = 8II$
tenuiloba		
var. *tenuliloba*	Strother (1969)	$n = 8, 13, 16II$*
var. *texana*		$n = 8II$
var. *treculi*		$n = 13, 16II$
var. *wrightii*		$n = 8II$
tephroleuca	Strother (1969)	$n = 8II$
Gymnolaena		
chiapasana	Strother (1983)	$n = 13II$
oaxacana	present paper	$n = 13II$
Leucatinia		
bracteata	present paper	$n = 16II$
Nicolletia		
edwardsii	(numerous workers!)	$n = 10II$
trifida		$n = 10II$
Pectis [40 or more species counted, all on a base of $x = 12$ (Keil, 1988)]		
Porophyllum		
calcicola	present paper	$n = 12II$
coloratum	Johnson (1969)	$n = 12II$
	Keil & Stuessy (1975)	$n = 12II$
crassifolium	Turner et al. 1973	$n = 15II$
gracile	(numerous authors)	$n = 24II$
greggii	Powell & Sikes (1970)	$n = 18II$
lanceolatum	Turner et al. 1979	$n = 22II$
linaria	present paper	$n = 12II$
macrocephalum	(numerous authors)	$n = 11II$
nelsonii	Strother (1983)	$n = 12II$
ochroleucum	Turner et al. (1973)	$n = 12II$
punctatum	(numerous authors)	$n = 12II$
ruderale	(numerous authors)	$n = 11, 22, II$

Most of the counts of *P. ruderale* have been $n = 22II$, but a few have been reported as $n = 11II$; the latter perhaps represent *P. macrocephalum*, which is often treated as part of *P. ruderale*).

scoparium	(numerous authors)	$n = 12II$
tridentatum	Johnson (1965)	$n = 15II$
	Reveal & Moran (1977)	$n = 15II$

(TABLE 2 continued)

Strotheria		
gypsophila	(several authors)	$n = 8II$
Tagetes spp.		$n = 11,12,18,24II$

About 30 species of this genus are reported in the literature: nearly all are on a base of $x = 12$ but *T. lucida* is consistently reported as $n = 11$ pairs; the only other anomalous count is for *T. signata* with $n = 18$ pairs, but this is presumably a triploid derivative, much as discussed for *Porophyllum greggii*].

Urbinella		
palmeri	Strother (1969)	$n = 8II$

*Strother (1989) has presented convincing evidence that the chromosome counts of $n = 13$ II in this taxon are miscounts of triploid individuals with $3x = 24$ (or seemingly diploids with $n =$ ca. 12 II).

seven genera, most having been recognized as subgenera and/or sections by previous authors. We list below those genera elevated by Strother, along with those species listed in his "nomenclator for *Dyssodia*" (1986, p. 376). Chromosome counts are from Table 2.

ADENOPHYLLUM
A. appendiculatum $n = 13$
A. cooperi $n = 13$
A. glandulosum $n = 13$
A. porophylloides $n = 13$
A. porophyllum $n = 13$
A. speciosum $n = 13$
A. squamosum no count
A. anomalum $n = 7$
A. wrightii $n = 7$

BOEBERASTRUM
B. anthemidifolia $n = 7$
B. littoralis $n = 7$

BEOBEROIDES
B. grandiflora no count

COMACLINIUM
C. montanum $n = 13$

DYSSODIOPSIS
D. tagetoides $n = 13$

DYSSODIA
D. decipiens $n = 13$
D. papposa $n = 13$
D. pinnata $n = 13$
D. sanguinea $n = 13$
D. tagetiflora $n = 13$

THYMOPHYLLA
T. acerosa $n = 8, 13$
T. aurantiaca no count
T. aurea $n = 8$
T. concinna $n = 8$
T. gentryi $n = 8$
T. gypsophila no count
T. micropoides $n = 8$
T. mutica no count
T. pentachaeta $n = 8, 13$
T. setifolia $n = 13$
T. tenuifolia $n = 8$
T. tenuiloba $n = 8$
T. tephroleuca $n = 8$

Chromosome numbers are now known for all of the generic segregates of *Dyssodia* except the monotypic *Boeberoides*. Even with this much narrower generic concept, counts on a base of both $x=7$ and 13 occur in *Adenophyllum*, and counts of both 8 and 13 occur in *Thymophylla* (presumably even within the same species, although this is discounted by Strother 1989). It would appear that the chromosome numbers provide little insight into relationships, unless, of course, those species of *Adenophyllum* with $n=7$ belong with *Boeberastrum*, or vice versa. It would seem best to view the various segregates as perhaps having an ancestral base number of $x=8$, and that $x=7$ is a dysploid derivative. Strother (1989) believes that at least some, if not all, of the counts of $x=13$ within *Thymophylla* are miscounts of sterile triploids (i.e., $2n=24$, the meiotic configurations appearing as $n=$ ca. 12 or 13). Nevertheless, the origin of species with $n=13$ pairs must be of long-standing, to judge by its distribution among at least four of the generic segregates from *Dyssodia*. But, looking at the broad picture, it would appear that species on a base of $x=13$ are largely confined to *Dyssodia* and closely related genera; hence, its occurrence in *Gymnolaena*, which has been placed within *Dyssodia* upon occasion. Indeed, considering its chromosome base, it would be reasonable to include *Gymnolaena* within *Dyssodia* (sensu lato).

Accepting *Dyssodia* in the broad sense, the most common base numbers in the Tageteae are $x=8$ and 12, the former occurring in four of the nine genera counted to date (*Dyssodia, Leucactinia*, *Strotheria* and *Urbinella*), the latter occurring in three of these (*Pectis, Porophyllum* and *Tagetes*). All of this would be simplified if one were to assume an *ancestral* base chromosome number of $x=4$ or 5; this would imply that numbers of $x=8$, 12 and 18 are 4x, 6x, and 9x respectively. Genera on a base of $x=5$ would include *Nicolletia* (2x), *Chrysactinea* (3x), and possibly the 2 taxa of *Porophyllum* (*P. crassifolium* and *P. tridentatum*) with $n=15$ pairs.

Most of the above is mere numerology. What is needed foremost is a detailed character-analysis of the tribe, perhaps with a sound cladistic analysis using *Chaetymenia* as an outgroup. This should be followed by a thorough chloroplast DNA analysis of the type performed by Jansen and Palmer (1988) to ascertain the likely reliability of the morphological systems proposed. Data from the latter workers (pers. comm.) suggest that the Tageteae is related to, or belongs within, the tribe Heliantheae (much as treated by Robinson, 1981, who recognized the Tageteae as but a subtribe within the Heliantheae). At present, chloroplast DNA studies on the Tageteae are limited, but such an approach will be needed before any confirmed new insights into phyletic relationships within the Tageteae is forthcoming. Until that time it would seem most prudent to retain the very familiar classificatory schemes, which would include a broad *Dyssodia*, as conceived by Strother (1969).

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